

THE SUBFAMILIES OF FORMICIDAE

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ABSTRACT—Eleven subfamilies are recognized and characterized. Ten of these are living—Dorylinae, Leptanillinae, Cerapachyinae, Myrmeciinae, Ponerinae, Pseudomyrmecinae, Myrmicinae, Aneuretinae, Dolichoderinae and Formicinae; one is extinct—Sphecomyrminae. An illustrated key is given for the workers of the ten living subfamilies.

Time was when a myrmecologist needed to know only five subfamilies of Formicidae. In 1910 W. M. Wheeler in his "Ants" recognized Ponerinae, Dorylinae, Myrmicinae, Dolichoderinae and Camponotinae. Emery kept this same scheme in the "Genera Insectorum" (1910-1925). It seems that the taxonomists of that day were averse to small taxa. The invertebrate zoologists, for example, were averse to small phyla; they preferred to tack a small group on to a large phylum as an appendix, i.e., with apologies, so to speak. The vertebrate zoologists kept the Agnatha, Chondrichthyes and Osteichthyes together as Class Pisces until fission was long overdue.

A sort of myrmecological independence was declared in 1920 when W. M. Wheeler split off the Cerapachyinae from the Ponerinae and the Pseudomyrmecinae (later emended to Pseudomyrmecinae) from the Myrmicinae. He also changed the name Camponotinae to Formicinae.

In 1923 W. M. Wheeler first suggested that the Leptanillini be separated from the Dorylinae; by 1932 their separation as Leptanillinae had been effected.

In 1951 Clark separated the tribe Myrmeciini from the Ponerinae to become subfamily Myrmeciinae. At the same time he suggested in a footnote that the Aneuretini in the Dolichoderinae be raised to subfamily rank. It was not, however, until 1956 that Wilson, Eisner, Wheeler and Wheeler made the promotion effective.

Finally, in 1967 Wilson, Carpenter and Brown described the extinct species *Sphecomyrma freyi* and based upon it the extinct subfamily Sphecomyrminae.

That makes 11 subfamilies.

CONSPECTUSES

In 1910 W. M. Wheeler had a conspectus of subfamilies and tribes (p. 134-144). In the "Genera Insectorum" Emery gave admirable characterizations of subfamilies, but they were scattered through 15 years and five fascicles. W. M. Wheeler (1922a) likewise gave excellent characterizations of seven subfamilies, but they were scattered

through 173 pages of text. Forel (1921:133-140) treated five subfamilies. The latest is that of Bernard (1951), but it can hardly be called a conspectus, because the characterizations are scattered through 47 pages (1040-1087) of text; furthermore he raised the eight subfamilies to family rank.

KEYS

In 1910 (p. 557) W. M. Wheeler presented a key to the five subfamilies and in 1922b (631-632) a key to the seven subfamilies. The latest cosmopolitan key is that of Clark (1951:14-16); he recognized 15 subfamilies, 5 of which are not accepted today.

None of the above mentioned is illustrated. In fact we have never seen an illustrated cosmopolitan key to the subfamilies of Formicidae. We present our version below. Few if any keys are perfect and this one is no exception: there are a few genera which will not key out; we have taken care of one such tribe, the Odontomachini, because it includes two large tropicopolitan genera.

SPHECOMYRMIDINAE

Workers.—Clypeus and frontal carinae simple but ant-like. Eyes large, convex, near the middle of the sides of the head. Ocelli large. Mandibles short, curvilinear, bidentate. Antennal scapes elongate (but shorter than usual in worker ants); funiculi long and filiform, the second segment the longest. Thoracic somites and epinotum separated from each other by 2 complete sutures; mesoscutum separated from mesoscutellum by a sunken area. Metapleural glands well-developed. Pedicel of a single segment, which bears a node. Sting well developed. Claws toothed.

This subfamily was established by Wilson, Carpenter and Brown in 1967 to include 1 extinct species in a new extinct genus, *Sphecomyrma freyi* from the Upper Cretaceous amber of New Jersey.

DORYLINAE

Workers.—Clypeus very short and not delimited by sutures. Frontal carinae vertical, close together or even fused, not covering the antennal insertions. Antennae short, of 7-12 segments, inserted near the mouth and quite close to each other. Eyes vestigial or absent. Palps 2- or 3-segmented. Sutures of thorax more or less effaced; metanotum concealed from above. Pedicel of 1 or 2 segments. Sting developed.

Females.—Dichthadiiform. Antennal segments 10-12. Eyes vestigial or absent; no ocelli. Sutures of thorax more or less effaced; metanotum concealed from above; wingless. Pedicel of 1 segment.

Males.—Mandibles developed, usually large. Antennae 13-segmented. Eyes and ocelli well developed. Winged; thoracic segmentation normal. Pedicel of 1 segment. Genitalia completely retractile; subgenital lamina forked. No cerci.

Larvae.—Elongate, slender, subcylindrical (but with a slight progressive attenua-

tion toward the anterior end); nearly straight (but with the anterior third slightly curved ventrally). Hairs short. Mandibles poorly developed and feebly sclerotized.

Pupae.—Worker pupae naked in *Aenictus* and *Neivamyrmex*, enclosed in cocoons in *Labidus* and *Eciton*; sexual pupae in cocoons.

These are the renowned army ants of the tropics (but they also occur in the southern parts of the Holarctic). They comprise about 165 species in 9 genera.

LEPTANILLINAE

Workers.—Minute to small; elongate and slender. Monomorphic. Clypeus forming a narrow straight border along the mouth. Mandibles straight and toothed. Maxillary palps 1- or 2-segmented; labial palps of 1 segment. Eyes absent. Antennae 12-segmented; not inserted close together. Promesonotal suture well marked; other dorsal sutures completely absent. Epinotum unarmed. Claws simple. Pedicel of 2 unequal nodiform segments.

Females.—Small. Eyes vestigial or lacking. Wingless. Pedicel of only 1 segment. Gaster long. Cloaca open.

Males.—Minute to small. Mandibles vestigial and toothless. Maxillary and labial palps prominent, of 1 segment. Eyes rather small, hairy, situated low on the head; ocelli conspicuous, on or near the occiput. Antennae 13-segmented; scape at most as long as the next 2 segments combined; funiculus filiform, the terminal segment the longest. Fore wings with few or no veins; stigma never well defined; hind wings veinless. Pedicel of 1 segment. Genitalia large, nonretractile; subgenital plate bifurcate.

Larvae.—Elongate and very slender; slightly constricted at the metathorax; anterior end curved ventrally; remainder of body straight and clavate. With a complex structure projecting anteroventrally from the venter of the prothorax. Only 1 pair of spiracles, which are on the third abdominal somite; each spiracle opening eccentrically on a naked circular area. Mandibles turned laterally; feebly sclerotized; each with a rather long slender sharp-pointed apical tooth which curves laterally; outer border of each mandible bearing several long slender sharp-pointed teeth.

This is a small (19 species in 4 genera) taxon, which is closely related to the Dorylinae. They are hypogeic, but little else is known about them. They have been taken in the Australian, Oriental and southern Palearctic Faunal Realms. The larvae are markedly different from all other known ant larvae.

CERAPACHYINAE

Workers.—Intermediate between Dorylinae and Ponerinae. Elongate, slender and subcylindrical. Antennal fossa more or less encircled by a lateral carina of the cheek (rarely obsolete); posterior surface of head usually with a distinct carina running ventrally from each dorsolateral corner. ~~Promesonotal suture distinct; other thoracic sutures obsolete.~~ Pedicel of 1 segment, which is nearly as broad as the thorax; first gastric somite separated by a well marked constriction from the second. Pygidium margined laterally and posteriorly with a row of large or small (but always distinct) spines. Sting developed.

Females.—Winged. Otherwise similar to workers (except dichthadiiform in *Acanthostichus*).

Males.—Mandibles developed. Winged. Genital armature completely retractile; subgenital lamina deeply and broadly furcate. No cerci.

Larvae.—Elongate, slender, subcylindrical and curved ventrally. Head small. Mouth parts large and prominent; bearing few or no spinules. Mandibles rather feebly sclerotized; typically long and slender; base moderately stout; distal $\frac{2}{3}$ narrow and thin; tapering to an apex which is slightly curved medially and posteriorly.

This small subfamily (64 species in 10 genera) is intermediate between the Dorylinae and the Poncrinae. It is primarily tropicopolitan but 4 species in 2 genera get up into the southern part of the Holarctic Realm.

MYRMECIINAE

Workers.—Head wide and short. Clypeus produced upward between the frontal carinae. Frontal carinae well separated, erect, not covering the antennal insertions. Mandibles very long, linear, narrow and sharp-pointed; masticatory border usually not distinct from basal border; entire masticatory border furnished with numerous unequal teeth. Maxillary palps of 6 segments, labial of 4. Antennae 12-segmented, slender and filiform. Eyes large; below the middle of the sides of the head. Thoracic sutures distinct; metanotum often distinct, its spiracles dorsal. Claws toothed. Epinotum unarmed. Pedicel 2-segmented; petiole nodiform or pedunculate with rounded node; postpetiole cup-shaped or bell-shaped, considerably larger than the petiole but still smaller than the following somite. Sting well developed.

Females.—Similar to workers but usually larger and winged; fore wing with 2 cubital cells and 1 discoidal cell. Mayrian and parapsidal furrows present.

Males.—Mandibles short and triangular; with very few teeth. Antennae 13-segmented; scape short; first funicular segment very short. Thorax, wings, pedicel and gaster as in the females. Pygidium rounded. Genitalia: stipes arched below, with a median dorsal appendage, styliform; volsella and lacinia present. Cerci developed.

Larvae.—Elongate, terete and rather slender; diameter diminishing gradually from the fifth abdominal somite to the anterior end; anterior half strongly curved ventrally. Body hairs simple, short and moderately abundant. Mandibles stout, subtriangular (in anterior view) and heavily sclerotized.

Pupae.—Enclosed in cocoons.

The Myrmeciinae are generally regarded as the most archaic living subfamily. Brown (1954:22-23) divided them into 3 tribes of 1 genus each: *Prionomyrmecini*, *Prionomyrmex*, 1 species from the Baltic Amber (Oligocene); *Nothomyrmecini*, *Nothomyrmecia*, 1 species (2 specimens) from Western Australia, which "appears to satisfy nearly all conditions demanded of an ancestral stock leading to the *Dolichoderinae* and *Formicinae*"; and *Myrmeciini*, *Myrmecia*, 96 species occurring in Australia and New Caledonia.

The workers range in length from 4 mm to 36 mm. The larger

species are called bulldog ants because of the "vicious way they attack and the tenacity with which their huge jaws hang on to their victim. All the workers and females are provided with a large sting with which they inflict a severe and painful wound. A burning sensation accompanied by redness and swelling may be felt at the wound some time afterwards and may last several days." (Clark 1951:18.)

PONERINAE

Workers.—Pedicel 1-segmented; first gastric somite demarcated from the second by a constriction (except in *Odontomachini*). Sting powerful.

Females.—Winged, the fore wing typically with 2 closed cubital cells. Otherwise similar to workers.

Males.—Winged, the fore wing typically with 2 closed cubital cells. Cerci present.

Larvae.—Varied according to genus, but usually primitive. Usually beset with numerous hairs or tubercles. Mandibles usually large, toothed and heavily sclerotized.

Pupae.—Enclosed in tough brown cocoons; callows capable of emerging without aid of workers.

This subfamily is a primitive but heterogeneous group of 530 species in 57 genera. It attains its greatest development in the Southern Hemisphere, but 13 genera range into the Holarctic Realm. The ponerines are eminently entomophagous. Colonies are usually small. Nests are in the soil or old logs, small and inconspicuous. The economic importance of the Ponerinae in the tropics can hardly be overestimated, since an estimated 80% of their food is termites.

PSEUDOMYRMECINAE

Workers.—Monomorphic. Elongate, often very slender. Clypeus with rounded upper margin, which is not prolonged upward between the frontal carinae (except in certain species of *Pseudomyrmex*). Frontal carinae usually subparallel and close together; generally narrow and not expanded laterally, thus leaving the antennal insertions fully exposed. Antennae short, 12-segmented. Ocelli usually developed. Pedicel 2-segmented, usually long. Sting well developed. Proventriculus developed anteriorly as an apple- or quince-shaped ball with 4 distinct sepals, which are bluntly rounded and hairy-tipped; developed posteriorly as a very short tubule projecting as a button into the cavity of the ventriculus.

Females.—Very similar to workers, except winged; wings with a discoidal cell and a closed radial cell; 2 closed cubital cells (except one in *Viticicola*).

Males.—Rather similar to workers, except winged. Antennae 12-segmented. External genitalia well developed, exserted. Cerci present.

Larvae.—Straight, slender, subcylindrical; ends rounded; somites distinct; head applied to the ventral surface near the anterior end. Near the mouth parts a swelling on each ventrolateral surface of each thoracic somite and the first abdominal somite. Trophophylax well developed. Mandibles rather small; apex stout and round-pointed.

Pupae.—Naked.

This is a small subfamily comprising 146 species in 4 genera. It is primarily tropical, but a few species in 2 genera enter the southernmost part of the Holarctic Realm. The *Pseudomyrmecinae* are almost exclusively arboreal and nest in plant cavities. The trophothylax is unique among ant larvae.

MYRMICINAE

Workers.—Monomorphic, dimorphic or polymorphic; dimorphism and polymorphism often very pronounced, the soldier phase with a very large head and strong mandibles. Frontal carinae large, nearly always covering the antennal insertions; nearly always well separated (rarely close together). Antennae of 4-12 segments; several terminal segments often forming a distinct club. Ocelli frequently lacking. Pedicel always 2-segmented. Sting developed in about half the species.

Females.—Winged. Larger than workers.

Males.—Winged. Mandibles usually developed. Antennae nearly always 13-segmented. Genitalia partially retractile (completely so in a few genera of *Solenopsis*).

Larvae.—Extremely heterogeneous as to shape, pilosity and mouth parts.

Pupae.—Always naked.

The Myrmicinae are the largest subfamily of Formicidae comprising 2000 species in 155 genera. As might be expected of so large a taxon, they are a cosmopolitan group, which is heterogeneous in both anatomy and habits, ranging from primitive to highly specialized. Among those specialized as to diet are the harvesters and the fungus-growers. The Myrmicinae also include most of the social parasites, which in extreme cases have lost their worker caste.

ANEURETINAE

Workers.—Integument comparatively thin and flexible. Clypeus broad, flat and emarginate below. Frontal carinae very short and only slightly elevated. Eyes below the middle of the sides of the head. Ocelli absent. Antennae 12-segmented; funiculus enlarging distally but not forming a distinct club. Thoracic sutures distinct; thorax impressed in front of the epinotum; metanotal spiracles forming a dorsal projection. Epinotum armed with 2 spines. Pedicel of a single segment, which is long, cylindrical and surmounted behind by a subglobular node. Sting developed. Proventriculus generalized, with simple mobile portal. Cloacal aperture slit-like and terminal.

Females.—Similar to workers, but winged and much larger. Fore wings with first radial crossvein lacking; Mf2 and Rs4 completely contracted. Ocelli well developed.

Males.—Similar to females but much smaller. Antennae 13-segmented, filiform.

Larvae.—Contrasted with *Dolichoderinae*: with a well developed neck, body hairy, mandibles large, heavily sclerotized, subtriangular (in anterior view) and bearing 2 rather large subapical medial teeth, maxillary palps and galeae paxilliform.

Pupae.—Enclosed in cocoons.

Subfamilies can get no smaller: 1 genus with 1 species—*Aneuretus simoni* of Ceylon. This genus was formerly placed apologetically in the Dolichoderinae but in a separate tribe. It is regarded as annectant between the Dolichoderinae and the Poncrinae. "There is evidence to suggest, and apparently none to deny, that the aneuretines represent the direct ancestors of the Dolichoderinae, and perhaps also of the Formicinae. At the same time it appears, on the important basis of external abdominal anatomy, that the aneuretines are more closely related to *Nothomyrmecia*, the living 'archetypal' myrmecine ant of Australia, than to any other primitive ant group." (Wilson, Eisner, Wheeler & Wheeler 1956:92.)

DOLICHODERINAE

Workers.—Integument usually relatively thin and flexible. Clypeus produced upward between the frontal carinae. Antennae of 12 segments (except 11 in *Semonius*) Metanotum participating in the thoracic dorsum; its spiracles often forming a dorsal protuberance. Pedicel of 1 segment, which is often surmounted by a scale. Cloacal opening a ventral transverse slit. Sting vestigial. A pair of anal vesicles into which unicellular anal glands empty their secretion; when irritated the worker expels the secretion, which becomes resinous in contact with air and gives off a characteristic aromatic odor.

Females.—Winged but otherwise similar to workers.

Males.—Winged. Antennae always 13-segmented.

Larvae.—Plump, chunky and turgid; straight or slightly curved; mostly subellipsoidal, with both ends broadly and equally rounded; anterior end formed by the enlarged dorsal portion of the prothorax; head ventral near the anterior end; no neck. Practically hairless; when present, hairs are few, short and usually simple. Mouth parts small; spinules sparse or absent. Mandibles small, feebly sclerotized; basal portion inflated; distal portion slender and acuminate, without teeth on the medial border (rarely a single small tooth). Maxillary palps and galeae represented by clusters of sensilla, never paxilliform.

Pupae.—Always naked.

This is a very homogeneous subfamily comprising 230 species in 19 genera. It is largely tropical, but 6 of the genera occur in the Holarctic Realm. The highly specialized larvae are fed with liquid food regurgitated by the workers.

FORMICINAE

Workers.—Integument relatively thin and flexible. Antennae of 8–12 segments; funiculus long and filiform, rarely forming a feebly developed club. Pedicel of 1 segment, which is usually surmounted by a scale. Sting vestigial. Poison glands converted into a cushion of convolutions; the poison (mostly formic acid) can be ejected with great force in certain genera (e.g., *Formica*) through a circular opening (the acidopore, which is not the cloacal opening) at the posterior end of the gaster; acidopore typically fringed with a circle of short fine hairs, which keeps the spray of poison directed outward away from the body.

Females.—Similar to workers, but much larger and winged. Wings with venation more or less reduced.

Males.—As large as females or smaller, generally similar; antennae of 10–13 segments; scape long (but exceptionally short in *Polyergus*);³ funiculus filiform (rarely forming a club).

Larvae.—Heterogeneous but mostly as follows. Thorax and first abdominal somite forming a distinct mobile neck, which is arched ventrally; remainder of body elongate, straight, subellipsoidal and rather slender. Body with a moderate to dense covering of short branched hairs. Mandibles small to moderately large; moderately sclerotized; subtriangular (in anterior view); wedge-shaped; apex forming a short blunt tooth, which is slightly curved medially; medial teeth absent or vestigial.

Pupae.—Usually enclosed in cocoons, but there are exceptions.

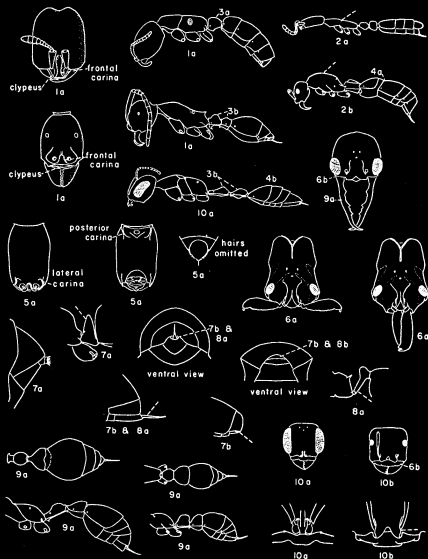
This next-to-largest subfamily comprises 43 genera and 1400 species (600 of which are in the genus *Camponotus*). It is a cosmopolitan taxon, which is dominant in temperate regions and common in the tropics.

"The members of this subfamily are morphologically the most highly developed of all ants; this is also true for their ethological peculiarities. Not only are their habits very diverse, but they show the most specialized form of mental and social behavior. The diet is in large part vegetarian and these ants show great predilection for sugary substances, which are sometimes stored in a special, replete form of worker (honey ants: *Melophorus*, *Myrmecocystus*, certain *Plagiolepis*, etc.). The species of *Oecophylla* and certain *Polyrhachis* and *Camponotus* build silk nests in leaves, using their larvae as silk-producing shuttles. Moreover, the nesting habits in this subfamily are very varied. Certain species of *Formica* and *Polyergus* are slave-makers; the species of *Polyergus* are true social parasites of *Formica*, entirely dependent upon their slaves but the worker caste is still present." (W. M. Wheeler 1922a: 211).

KEY TO THE SUBFAMILIES OF FORMICIDAE

(Based on the workers. Living subfamilies only. The numbers and letters on the figures correspond with half-couplets in the key.)

- 1a. Eyes absent or vestigial; pedicel usually of two segments in the worker (one in female and male); clypeus short; frontal carinae short and vertical, not covering the antennal insertions; antennae usually short, epinotum usually unarmed 2
- 1b. Without this combination of characters 3
- 2a. Promesotal suture distinct; minute to small (2.5 mm long or less); elongate and slender; maxillary palps of one or two segments, labial palps one-segmented *Leptanillinae*
- 2b. Promesonatal suture weak or absent; palps of two or three segments *Dorylinae*



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| 3a. Pedicel of one segment | 4 |
| 3b. Pedicel of two segments | 9 |
| 4a. With a conspicuous constriction between 1st and 2nd gastric segments | 5 |
| 4b. Without a constriction between 1st and 2nd gastric segments | 6 |
| 5a. Elongate, slender and subcylindrical; scape usually short and stout; antennal fossa more or less encircled by a lateral carina on the cheek (rarely | |

- obsolete); posterior surface of head usually with a distinct carina running ventrally from each dorsolateral corner; dorsal surface of thorax with sutures indistinct or absent; pygidium margined laterally and posteriorly, with a row of large or small (but always distinct) spines *Cerapachyinae*
- 5b. Without this combination of characters *Ponerinae*
- 6a. Mandibles articulated near the middle of the ventral border of the head; when closed, parallel to each other; when fully open, they form together a straight line parallel to the ventral border of the head. Tribe Odontomachini in the *Ponerinae*
- 6b. Mandibles articulated to the ventral corners of the head 7
- 7a. Opening at posterior end of gaster (acidopore) terminal, circular and usually surrounded by a fringe of hairs; sting vestigial; petiole usually scale-like *Formicinae*
- 7b. Opening at posterior end of gaster (cloacal orifice) slit-like 8
- 8a. Sting well developed and protrusible; anterior peduncle of petiole long and cylindrical; node subglobular *Aneuretinae*
- 8b. Sting vestigial; petiole not as above *Dolichoderinae*
- 9a. Mandibles very long, linear, narrow and sharp-pointed, the entire medial border furnished with teeth; epinotum unarmed; petiole nodiform or pedunculate with rounded node; postpetiole cup-shaped or bell-shaped, considerably larger than the petiole but still smaller than the following somite; eyes below the middle of the sides of the head *Myrmecinae*
- 9b. Without this combination of characters 10
- 10a. Elongate, often very slender; eyes very large and elongate; clypeus with a rounded upper margin, not prolonged upward between the frontal carinae; frontal carinae usually close together, usually narrow and not expanded laterally to cover the antennal insertions; antennae short *Pseudomyrmecinae*
- 10b. Without this combination of characters; frontal carinae usually large, nearly always covering the antennal insertions and nearly always well separated *Myrmicinae*

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